Investigating the potential for call combinations in a life-long vocal learner.

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ABSTRACT

The ability for humans to create seemingly infinite meaning from a finite set of sounds has likely been a critical component in our success as a species, allowing the unbounded communication of information. Syntax, the combining of meaningful sounds into phrases, is one of the primary features of language that enables this extensive expressivity. The evolutionary history of syntax, however, remains largely debated, and it is only very recently that comparative data for syntax in animals has been revealed. Here, we provide further evidence for a structural basis of potential syntactic-like call combinations in the vocal communication system of a group-living songbird. Acoustic analyses indicate that Western Australian magpies (*Cracticus tibicen dorsalis*) structurally combine generic alarm calls with acoustically distinct alert calls to produce an alarm-alert sequence. These results are distinct from previous examples of call combinations as, to our knowledge, evidence for this capacity is yet to be demonstrated in a non-human species that is capable of vocal learning throughout life. These findings offer prospects for experimental investigation into the presence and function of magpie call combinations, extending our understanding of animal vocal complexity.

Keywords: call combinations, syntax, animal vocal communication, language evolution, Western Australian magpie, Cracticus tibicen dorsalis.

1. Introduction

The immensely generative nature of language has long been thought to be a key factor distinguishing humans from other animals (Collier et al., 2014; Hurford, 2011). The property of language that enables extensive combinatorial power is known as double articulation and refers to the combining of sounds into words (phonology), and the grammatical combining of meaningful words into phrases (syntax, Hurford, 2011). While there is no doubt humans are capable of vast combinatorial power (Hurford, 2012), recent comparative research has begun to draw parallels between language's combinatoriality and potential equivalents within non-human animal vocal communication systems (Arnold & Zuberbühler, 2006; Engesser et al., 2016; Ouattara et al., 2009; Suzuki et al., 2016; Townsend et al., 2018).

Many non-human animals, such as some cetacean and avian species for example, have been found capable of stringing sounds together into larger sequences, that, at least superficially, are reminiscent of the phonological layer of human language (Engesser et al., 2015; Hauser et al., 2002; Suzuki et al., 2006; Tyack, 1983). Moreover, a growing body of work has revealed interesting potential homologous and analogous examples of call combinations in animals which can be feasibly compared with simple syntactic structures in language (Arnold & Zuberbühler, 2006; Ouattara et al., 2009; Townsend et al., 2018).

The combination of context- specific calls into a meaningful sequence has been suggested in two different studies in related monkey taxa (Arnold & Zuberbühler, 2006; Ouattara et al., 2009). Putty-nosed monkeys (*Cercopithicus nictitans*) combine two predator-specific alert calls into a larger meaningful sequence (Arnold & Zuberbühler, 2006). However, despite the discrete calls each being elicited upon discovery of the presence of a specific predator, the sequence evokes group movement regardless of predatory context. It is, therefore, uncertain whether this call sequence is indicative of compositional or instead combinatorial syntax, where the meaning of the resultant sequence (i.e. 'Let's go') is not a product of the combination of the alarm calls' meanings (Collier et al., 2014; Hurford, 2012).

Perhaps more convincing evidence of rudimentary compositional syntax in primates is shown in a study on male Campbell's monkeys (*Cercopithecus campbelli campbelli*), where the use of an acoustically invariant suffix modifies the meaning of predator-specific alarm calls in a predictable way (from more specific to more general, Ouattara et al., 2009). Specifically, this has been argued to be akin to abstract meaning operators in language, such as "like", that generalises the meaning of words ("monkey" to "monkey-like") and is therefore suggestive of basic compositional syntax (Collier et al., 2014; see also Townsend et al., 2018).

Recently, additional evidence of simple syntax has been seen in more distantly related species. The combining of warning and recruitment calls in the Japanese great tit (*Parus minor*) elicits a compound response consisting of a combination of the behaviours prompted by each individual call (Suzuki et al., 2016). Critically, when artificially reversing the sequence, the authors find a change in behavioural response, which is argued to indicate the sequence is perceived as a single meaningful unit (Suzuki et al., 2016). Similarly, alert and

recruitment calls in the cooperatively breeding southern pied babbler (*Turdoides bicolor*) are combined into a sequence eliciting mobbing behaviour from conspecifics in the presence of a territorial threat (Engesser et al., 2016). Experiments demonstrated that the individual calls have an independent meaning that are distinct from, but contribute to, the meaning of the mobbing sequence and thus are strongly indicative of rudimentary syntax (Engesser et al., 2016; see Suzuki et al., 2018, Townsend et al., 2018 and Zuidema & de Boer, 2018). These studies have laid the foundation for further research into basic syntactic abilities in non-human animals.

In this study, we build on emerging evidence of avian syntactic abilities by investigating the occurrence of call combinations in the Western Australian magpie. Magpies in south-western Australia are highly territorial, and cooperatively defend a year-round territory (Ashton et al., 2018; Farabaugh & Brown, 1988; Hughes et al., 1996). All group members participate in territorial defence behaviours throughout the year, including vocalizations, inter-group fighting, and aggressive posturing (Farabaugh & Brown, 1988; Kaplan, 2004; Kaplan, 2006; Kaplan et al., 2009). Both sexes have a similarly well-developed song and extensive vocal repertoire (Kaplan, 2005; Suthers et al., 2011; Walsh, 2017). Males do not use song or any other specific vocalization for courtship and thus share the same basic repertoire with females (Kaplan, 2005).

The vocal repertoire of adult Western Australian magpies (hereafter magpies) can be separated into short alarm calls, distress or alert calls, begging, feeding grunts, and carols or warbling calls (Baker, 2009; Kaplan, 2004; Silvestri, 2017; Walsh, 2017).Previous research has revealed the potential for context specificity in a variety of magpie vocalizations, such as

carols and some alarm calls (Baker, 2009; Kaplan, 2008). For example, carolling calls may signal territoriality and willingness to participate in defence of the group territory (Baker, 2009). Furthermore, there is evidence that some alarm calls may be predator specific in nature (Kaplan, 2005; Kaplan, 2006; Kaplan, 2008; Kaplan et al., 2009; Kaplan & Rogers, 2013). In light of the context-specific nature of magpie calls (Kaplan, 2008), and due to the clear capabilities for flexibility in call structure (Kaplan, 2000), we reasoned rudimentary syntactic structuring might also exist in the vocal system of magpies. While basic combinatoriality in magpie vocal communication has been alluded to in past research (Kaplan, 2005) to date, systematic investigations have not been conducted.

Moreover, to our knowledge, syntactic capabilities have not yet been indicated in a life-long vocal learner other than humans. Magpies have been shown to be capable of flexibly interspersing mimicry into their own song, indicating a high plasticity of vocal learning and high retention of learned material throughout life (Brown & Farabaugh, 1991; Kaplan, 2000; Kaplan, 2005). The fact that magpies can be considered as open-ended vocal learners is particularly interesting because theory suggests that the transition from a non-compositional system to a compositional one, relates to a constraint in the number of available calls (Nowack, 2000). As this would seemingly not be a constraint for a life-long vocal learner, if syntactic capability is revealed in magpies it could provide additional insight into the potential evolutionary forces promoting the progression of syntax.

One instrumental first step prior to unambiguously identifying a syntactic-like combination in non-human animal communication systems involves isolating naturally-occurring, stereotyped, call combinations and then demonstrating that the calls comprising the

combination and the same calls produced alone are acoustically equivalent (*sensu* Hedwig et al., 2014), such that the combination can be feasibly be considered as composed of independently-occurring calls (see Hedwig et al., 2015, Engesser et al., 2016 & Suzuki et al., 2016).

Observational work has indicated that magpies do indeed produce such a sequence in the form of an "alarm-alert sequence" appearing to be comprised of two independently occurring calls, a generic alarm call and an alert vocalisation (Figure 1), and used in a variety of threat-related contexts. Furthermore, field observations suggest the call may convey information to receivers with individuals responding predominantly with vigilance-type behaviours such as scanning, vigilance, mobbing a predator, and movement directly following the call (Walsh, 2017). Regarding the individual call types, observations indicated alarm calls produced predominantly during the approach of humans, dogs and general disturbance (Silvestri, 2017; Walsh, 2017). The alert call, however, coincides with the presence of a potential predatory threat, often eliciting response behaviours such as vigilance, scanning or carolling vocalisations from other group members (Silvestri, 2017; Walsh, 2017).

The fact that two independently occurring calls (alarm and alert calls) are concatenated into a single structure (alarm-alert sequence) is suggestive that the call might represent a syntactic-like structure (Hurford, 2011), providing a solid basis for the investigation into this combinatorial ability (Townsend et al., 2018). Here, we provide the first step in demonstrating that magpies may be capable of producing call combinations by quantifying the extent to which the calls comprising the combination are (a) acoustically distinct units and (b) acoustically equivalent to those produced alone.

2. Methods

2.1. Study site and animals

Fourteen groups of free-living magpies were chosen for this study. The groups were situated in the urban Perth suburbs of Guildford (31°89'S, 115°96'E) and Crawley (31°98'S, 115°81'E), within Western Australia. Many individuals within these groups have been ringed for identification and are habituated to human presence, therefore allowing observation and vocal recording at a close distance (Ashton et al., 2018; Edwards et al., 2015; Mirville et al., 2016).

2.2. Natural observations and acoustic recording

We recorded naturally occurring vocalizations and the context in which they were given, while following groups in the field to compile a database of independent calls and potential call combinations. Vocalizations were recorded at a 44.1 kHz sampling rate using a Roland R-05 digital wave/mp3 recorder coupled to a Rode NTG2 directional condenser microphone encased in a Rode Blimp Suspension Windshield. Data collection was conducted during observations sessions (4-6 hours/session) on 27 days between June and August 2017. Data was primarily collected in the morning to coincide with the higher activity levels of magpies (Edwards et al., 2015). Recording focused on adult magpies, with no restriction based on sex.

We obtained over 500 recordings of distinct magpie vocalizations, which were extracted from

~150 hours spent following groups in the field. The recordings we obtained were added to a sound database that already contained over 2000 recordings (~12 hours of raw material) collected by the University of Western Australia's (UWA) magpie research group from 2014 to 2017. Within the database, the independent vocalizations were categorised into the following call types based primarily on auditory and observational features; begging, feeding grunt, alarm, alert, carol, chorus (more than two individuals carolling at the same time), and mimicry. Within each call type, calls were then further categorised into similar acoustic units based on visual (spectrographic) features. The following contextual details were logged where possible for each recording; caller identity and behaviour immediately prior to/following vocalization, group members present, stimulus or disturbance, and group response (vocal and behavioural).

Periods of silence have been used as a method of classifying boundaries between acoustic units in numerous previous studies, including research on birdsong in zebra finches (*Taeniopygia guttata*, Franz & Goller, 2002), killer whale (*Orcinus orca*) calls (Shapiro, 2011), and gorilla (*Gorilla beringei beringei* & *G. gorilla gorilla*) close calls (Hedwig et al., 2014). Previous research on magpie song production indicated duration of mini-breaths between song syllables to be roughly < 0.3 seconds (Suthers et al., 2011). As this study focussed on alarm and alert calls rather than song production, we have slightly increased the period of silence between calls to reflect the observed trend in periods of silence in call series (independent calls produced consecutively) versus call combinations (two or more calls produced in concatenation). As such, in this study, we defined calls as either discrete calls (singular independent units separated by a period of silence equal to or greater than 0.5 seconds) or potential call combinations (independent units separated by a period of silence

less that 0.5 seconds). This is based on visual inspection of spectrograms of individual calls, discrete call series, and potential call combinations.

A subset database was created focussing on the calls that, from preliminary field observation and acoustic investigation, were (a) given frequently and (b) flexibly combined into a larger sequence (see Figure 2 for examples). The subset database included the number of recordings obtained for each call type from each individual from each group, and their respective observational contexts. From the subset database, one type of alarm-alert sequence (Figure 1) was chosen for acoustic analysis. This sequence was chosen based on the number of different groups recorded producing this vocalization (N=11) and the high frequency of occurrence of this sequence (and its comprising calls) detected during observational research.

2.3. Acoustic analysis

Calls were assessed for quality (where high quality = high signal to background noise ratio), and the percentage of the call demonstrating clear, tonal structures using Audacity 2.1.2 (Audacity Team, 2016). Due to a limitation in the number of good-quality recordings of each discrete call type in all test groups, only 26 recordings of the alarm, 9 recordings of the alert and 19 recordings of the alert-alarm sequence, were used for analysis (our study site is located within an urban matrix and so many recordings were compromised by background noise). Spectrographic cross-correlation (SPCC) analyses were run to compare the recordings within each call-type to determine if the calls were correlated. Analyses were then undertaken to determine if the two calls are distinct in structure, and to compare the recordings of discrete calls with the respective sequence component to determine similarity in structure.

SPCC compares the structural features in time-frequency spectrograms of two calls or sounds, taking a peak correlation value as a measure of similarity and generating a matrix of similarity values for each pair of calls in the analysis (Cortopassi & Bradbury, 2012).

To verify that alarm and alert calls are independent units that are structurally distinct from each other, both the discrete calls and their respective sequence components were cross-correlated with the other call type using SPCC. A procedure based on the Mantel test was then used to test the null hypothesis that the calls grouped into the alarm or alert categories were no more similar to other calls within their own group than to calls within the other call-type group. As such, the SPCC matrix was compared with a second 'hypothesis' matrix which contained a binary code, whereby '1' represented same-group comparisons and '0' represented different-group comparisons in equivalent positions ('group' is defined as the recording being either an alarm or alert call, Schnell et al., 1985). A p-value less than the alpha (set at 0.05) indicates the two calls are structurally distinct.

SPCC and Mantel testing were then used to test the null hypothesis that the discrete calls were no more similar to each other than to their respective component in the call sequence, using the same protocol as described above (Schnell et al., 1985). A p-value > 0.05 indicates the structure of the discrete call is similar to the structure of its respective sequence component, therefore confirming the two discrete calls are structurally combined into a sequence.

All SPCC analyses were conducted using Batch Correlation Analysis in Raven (Bioacoustics Research Program, Cornell University, Ithaca, 2017) using normalized Hamming window

spectrographic correlation analysis on peak values, with a band pass filter from 500Hz to 22,000Hz.

3. Results

Spectrographic cross-correlation analyses revealed distinct call structure, with calls correlated within each call-type. The mean correlation coefficient was consistent across cross-comparisons of alarm calls (SPCC: $\bar{x} = 0.30$, n = 325), alert calls (SPCC: $\bar{x} = 0.34$, n = 36), and alarm-alert sequences (SPCC: $\bar{x} = 0.34$, n = 171).

Mantel tests comparing correlation coefficients for alarm and alert call-type comparisons were highly significant (10,000 permutations, $r = 0.284$, $p < 0.0001$), indicating the two calls (alert and alarm) are structurally distinct from one another (Table 1).

Pairwise comparison analysis indicated the two discrete calls were correlated with their respective sequence counter-parts. Mantel tests comparing correlation coefficients from pairwise comparisons of each of the discrete calls with their respective cut-sequence components were non-significant for both alarm (10,000 permutations, $r = 0.022$, $p = 0.488$) and alert calls (10,000 permutations, $r = 0.019$, $p = 0.706$) (Figure 3, Table 1). Therefore, recordings of the discrete calls were no more similar to one another than to their respective component cut from the sequence.

4. Discussion

Using acoustic analyses, we investigated a potential call combination in the Western Australian magpie. Our results indicate that the alarm and alert calls are both acoustically distinct from one another but similar in structure to their respective sequence counterparts. Furthermore, spectrographic correlation analyses revealed similarity across recordings from multiple individuals, of the alarm, alert and sequence calls. These results provide evidence that the alarm and alert calls are distinct, highly repeatable calls that occur across all study groups and, at least at the structural level, are combined into an alarm-alert sequence.

The extent to which the detected combination of alarm and alert calls in the Western Australian magpie represents a syntactic-like structure, however, requires follow up experimental verification. Such experiments are key to unpacking the function of the independent calls and the combination via assessing receiver response in the absence of the stimuli that naturally elicit the vocalisations (*see* Suzuki et al., 2016 & Engesser et al., 2016).

Furthermore, although initial evidence is provided here for one potential call combination, preliminary observational data indicate magpies may be capable of flexibly creating combinations larger than a two-call construction, which has, to our knowledge, yet to be demonstrated in a non-human animal communication system (see Figure 2 e-h for potential examples, Russell & Townsend, 2017). Hence, follow up work is critical to assess the extent to which (a) magpies use call combinations, (b) whether these combinations are functionally relevant and meaningful to receivers, and (c) whether these combinations are indeed indicative of compositional syntax, or rather combinatoriality.

Our finding of a candidate call combination in magpies (if validated under future experimental investigation), in addition to previous research indicating similar rudimentary compositionality in primates (Ouattara et al., 2009) and other bird species (Engesser et al., 2016; Suzuki et al., 2016), further suggests that the capability for syntactic-like structuring in vocal communication is not confined to humans, and may instead be phylogenetically widespread (Collier et al., 2014). Such research can aid in bridging the gap between human and animal communication, and potentially shed light on the evolutionary development of complex vocal communication systems (Russell & Townsend, 2017).

It has been hypothesized that a transition to syntax may have evolved as a result of natural selection favouring the combining of meaningful calls when the number of relevant events needing to be communicated exceeds the number of calls available (Nowack et al., 2000). Thereafter, simple two-word or sign combinations may have occurred as a means of increasing lexicon size (Russell & Townsend, 2017). Interestingly, previous and ongoing work suggests magpies' already have an extensive vocal repertoire facilitated in part by their capacity to vocally imitate (Brown & Farabaugh, 1997; Kaplan, 2005; Suthers et al., 2011). Why magpies would need to combine calls to communicate new events if they could instead incorporate a new call/sound into their repertoire is therefore unclear. A bias towards combinatoriality could, in principle, be driven by working memory constraints on the part of the receiver: deriving meaning compositionally places less load on working memory than learning and storing a new call type (Nowack et al., 2000). Further work investigating the processing of calls will help shed light on the pressures driving combinatoriality in magpies, which in turn has the potential to shed light on the evolution of human syntax given that humans are also open-ended vocal production learners.

Investigating the presence of combinatoriality in animals is a critical first step to understanding the origins and phylogenetic spread of this key linguistic ability. Our results demonstrating combinatorial structures in Western Australian magpies contributes to recent work showing that avian species are capable of producing and processing call combinations (Engesser et al., 2016; Suzuki et al., 2016), in turn indicating that the phylogenetic spread of this capacity is greater than previously thought. Critically, our research provides important initial evidence of the presence of call combinations in a vocal learning species (excluding *Homo sapiens*), which has interesting implications for theories explaining the evolution of combinatoriality more generally. These results set the foundation for further experimental investigations into syntactic-like structures in this species – a vital step in furthering our understanding of this largely enigmatic field (Suzuki et al., 2018; Townsend et al., 2018).

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TABLE

Table 1. Comparisons of different calls types using Mantel test.

Comparison	Mean Correlation	r	*P*
Alarm vs Sequence-Cut Alarm	0.315	0.022	0.488
Alert vs Sequence-Cut Alert	0.355	0.019	0.706
Alarm vs Alert	0.269	0.284	<0.0001*

Mantel tests were based on correlation coefficients obtained from SPCC on discrete calls versus respective sequence components and alarm call versus alert call. 18 recordings of each sequence-cut call, 26 recordings of alarm calls, and 9 recordings of alert calls were used in analysis. Asterisks indicates significant difference in call comparison whereby $p<0.05$.

FIGURE LEGENDS

Figure 1. Spectrograms of the independent (a) alarm and (b) alert calls, and the (c) sequence they comprise which was used for acoustic analysis. Calls are separated into independent units (indicated by black lines) based on their occurrence with a period of at least 0.5 second of silence in between calls.

Figure 2. Spectrograms of magpie alarm (a & b), alert (c & d) calls and potential call combinations (e-h). Calls are separated into independent units (indicated by black lines) based on their occurrence with a period of at least 0.5 second of silence in between calls.

Figure 3. Distribution of correlation coefficients obtained from SPCC on pairwise comparison of each alarm and alert call-types. Calls were correlated within each call-type. Boxes show the medians and interquartile ranges, and whiskers show the ranges (n = number of comparisons).